Rocky Mountains

Southwest

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Vigor of Ponderosa Pine Trees Surviving Mountain Pine Beetle Attack

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Some ponderosa pine trees survived attack by mountain pine beetles, even though their sapwood was partially blocked by blue-stain fungi. Seven years after a beetle outbreak in the Colorado Front Range, these trees had decreased foliage area and radial growth, indicating low vigor. These surviving trees should be considered for removal during salvage logging operations.

Keywords: *Pinus ponderosa, Dendroctonus ponderosae,* forest entomology, silviculture

Management Implications

Outbreaks of mountain pine beetles in ponderosa pine stands kill many trees 20 to 40 cm in diameter. However, some trees survive the attack, even though the sapwood of these trees usually is infected with blue-stain fungi.

Although the blue-stain infection is not extensive enough to completely block the sapwood and kill these trees, the water-conducting capacity of the sapwood apparently is sharply reduced. Consequently, the foliage area of trees surviving attack is reduced through physiological feedback mechanisms; this greatly reduces radial growth and overall vigor.

In the observations reported here, no evidence was found 7 years after attack that the vigor of these trees was improving. Therefore, if dead trees are removed by salvage logging, surviving, attacked trees also can be removed with little effect on stand growth, although aesthetic considerations may be important. Surviving, attacked trees can be recognized using the crown vigor rating system presented here and by noting the presence of pitch tubes on the bole.

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Introduction

In severe outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins), more than 40% of the ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) trees in the 20- to 40-cm d.b.h. class often are killed (McCambridge et al. 1982). Not all attacked trees are killed, however. Many of the surviving, attacked trees (termed "pitchouts" by foresters) appear to be in poor vigor for years following the attack. Pitchouts can be identified by the presence of pitch tubes scattered over the trunk (McCambridge et al. 1979). Pitch tubes are resin exudations formed as attacked trees respond to trauma resulting from beetle entry. Large pitch tubes generally indicate strong tree resistance; small ones are usually associated with a relative lack of resistance. Pitch tube color on pitchouts varies from whitish when fresh to yellow when weathered.

The killed ponderosa pine trees have succumbed to the combined effects of the beetles and blue-stain fungi that the beetles introduce (Shrimpton 1978). After attack, the fungi rapidly spread through the sapwood, often completely plugging the sapwood in a matter of days. The crowns of these trees appear to have had their water supply rapidly interrupted. This condition is consistent with results reported by Horntvedt et al. (1983) and Paine (1984), who showed that water stress increased in conifers inoculated with blue-stain fungi.

A mountain pine beetle outbreak began in 1974 in the montane zone of the Colorado Front Range. In the study area, the epidemic years were 1976 to 1978. Several years after the attack, it was apparent that some of the surviving trees had poor vigor. It was hypothesized that the poor vigor trees became infested with blue-stain fungi, but the progress of the fungal infection was arrested before the sapwood conducting tissue was completely blocked.

If this hypothesis is true, water transport phenomena and the physiological necessity for plants to keep in balance the relative size of different parts of the water transport pathway may account for the poor vigor of some of the surviving trees. In healthy trees, the size of the absorbing root system, sapwood conducting tissue, and transpiring surface remains in balance (Kaufmann and Troendle 1981). This physiological balance is maintained by feedback mechanisms. In trees having partially blocked sapwood conducting tissue, foliage area is reduced by regularly-occurring water stress above the blockage. This decreases photosynthesis, and, in turn, bole diameter growth and root growth.

This study compared attacked trees having poor vigor with healthy, apparently unattacked trees having no pitch tubes on the boles. The comparison involved observations related to the physiological capacity of the trees to grow, including an evaluation of the quantity of foliage on branches and the presence of blue-stain fungi in the sapwood (commonly *Ceratocystis montia* (Rumb.) Hunt and *Europhium clavigerum* Robinson-Jeffrey and Davidson) (Davidson 1979).

Methods and Materials

Studies were conducted about 20 km southwest of Fort Collins, Colo., at an elevation of about 2,000 m. In June 1983, trees were sampled along a small ridge oriented northeast to southwest. About 40% of the trees along the ridge had been killed during the beetle outbreak (typical for a severely attacked area). Of the surviving trees, 10–20% were attacked and survived.

A total of 10 tree pairs were selected by appearance, size, and location. Each pair included one tree which had survived the beetle attack, as evidenced by typical pitch tubes. The attacked trees also were characterized by "tufted" foliage, in which the needles were clustered near the end of the branches. The other tree of each pair was approximately the same size and age, and was within 20 m of the surviving tree on a similar site. These trees had no evidence of beetle attack and appeared much more vigorous, with slightly longer needles which extended along a larger portion of each branch.

Measurements on each tree included age and diameter at breast height, height, and, for attacked trees, the number of pitchout tubes 1 to 2 m above the ground. Radial growth during the previous 5 years (1978–82) was determined on four increment cores taken at breast height. A dissecting scope was used to examine the cores for the presence of blue-stain fungus. The total thickness of the sapwood and the portion of the sapwood darkened by the fungus were determined.

Representative branches were removed from the crown of each tree with a pole pruner. The length from the branch tip over which live needles were attached was determined, as was the number of individual needles per centimeter for the middle 5 cm of the branch portion having live needles. Average needle length and the age of the oldest needles on the branch also were determined. All results were evaluated using a standard t-test for paired samples.

During the observations, it became apparent that crown appearances differed substantially. Vigorous trees had dense crowns, and needles in the upper half of the crown extended back 30 to 50 cm from each branch tip. Trees appearing the least vigorous had very open crowns and live needles along only about 10 cm of each branch tip.

Therefore, a visual rating system was devised in which two observers estimated (to the nearest 10 cm) how far back from the branch tip live needles extended, on branches located about one-third of the distance down from the top of the live crown. Branches having 45 to 55 cm of length with live needles were given a rating of 5, and branches with 5 to 15 cm were rated 1. Figure 1 illustrates the appearance of typical crowns for ratings of 1 to 5. The crowns of 41 trees were rated visually along a 200- to 300-m transect. After each crown was rated, the number of pitch tubes on the bole 0 to 4 m above the ground was determined, allowing a comparison of crown vigor with apparent intensity of beetle attack.

Trees surviving attack by mountain pine beetles were distinguished from trees undergoing recurrent attack by ponderosa pine needle miners (*Coleotechnites ponderosae* Hodges and Stevens). Needle miners infest foliage older than the current year's growth (Stevens and Leatherman 1982); infested needles characteristically are green at the base but brown and dead beyond the point of internal feeding by the larvae. Frequently, only the current year's foliage appears normal. In contrast, trees attacked by mountain pine beetles have nearly normal needles retained for 4 or more years, although the annual branch length growth usually is reduced. Furthermore, trees attacked by mountain pine beetles have pitch tubes, while those infested with needle miners do not.

Results

Most of the study trees on which needle and radial growth were measured were 50 to 80 years old, 15 to 30 cm d.b.h., and 8 to 11 m tall, although several trees were outside these ranges (table 1). On trees having poor crown appearance and apparently poor vigor, from 7 to 70 pitch tubes were observed in the bole section 1 to 2 m above the ground. These trees showed clear evidence of mountain pine beetle attack. In contrast, the apparently vigorous trees had no readily-seen pitch tubes and did not appear to be attacked.

Surviving, attacked trees had evidence of blue-stain fungus in 9 of 10 cases, and staining reduced the clear sapwood in the increment cores to as low as 20% (table

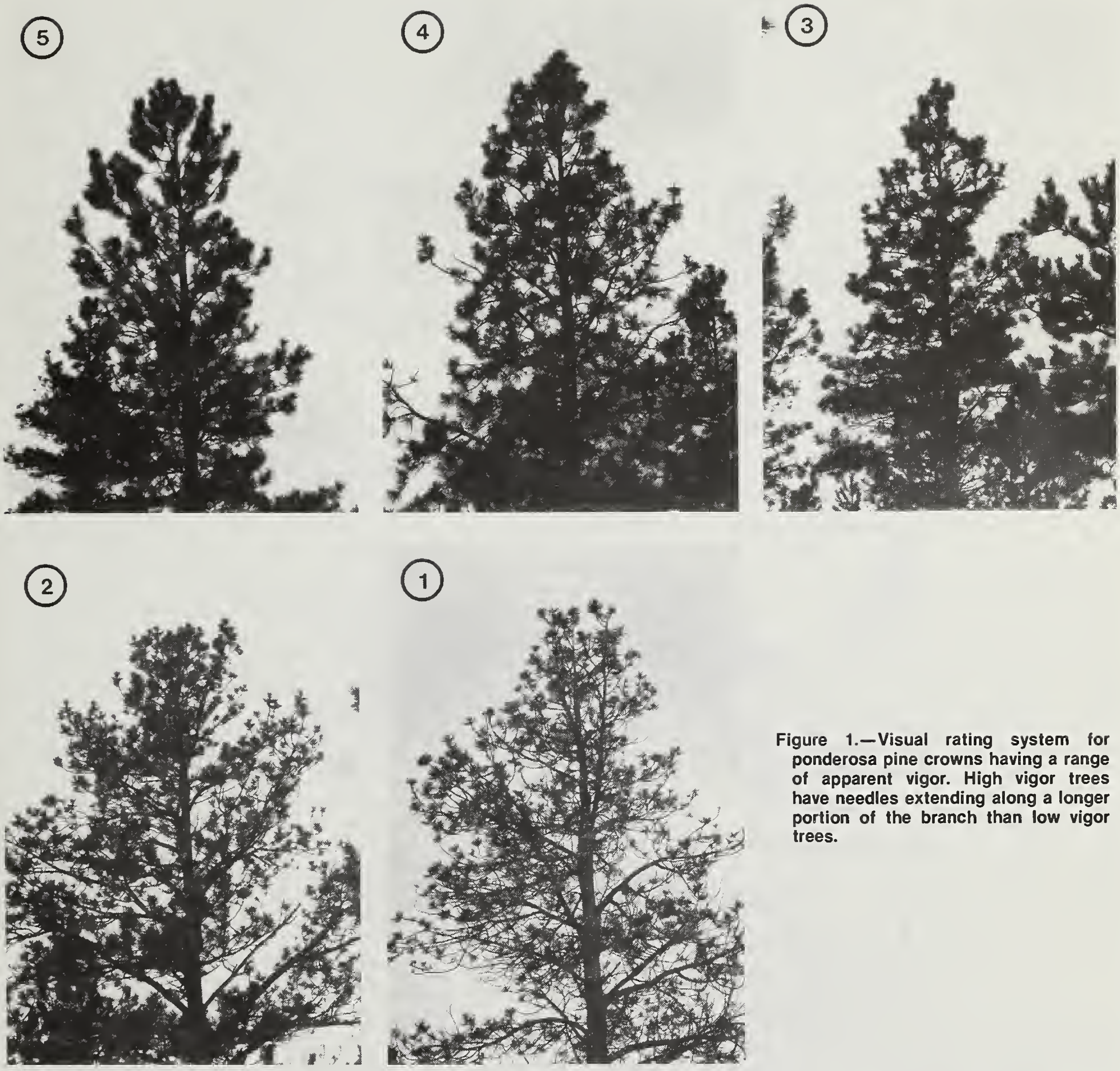

Figure 1.—Visual rating system for ponderosa pine crowns having a range of apparent vigor. High vigor trees have needles extending along a longer portion of the branch than low vigor trees.

2). The average amount of clear sapwood in cores taken from the poor vigor trees was 74.4% of the total sapwood length in the cores. The blue stain occurred at various positions in the sapwood. No staining was observed in the trees having good vigor.

On trees having healthy crowns, live needles extended about 30 cm back from the branch tip (table 2). However, on poor vigor trees, needles were found only along the terminal 11 cm, resulting in a tufted appearance throughout the crown (fig. 1). Mean needle length of poor vigor trees was reduced 19% compared to that of healthy trees, but the number of needles per cm of branch length was not affected. Needles were retained for an average of 5.8 years for healthy trees, compared with 4.6 years for poor vigor trees.

Radial growth during the most recent 5 years prior to sampling (1978–82) was reduced 34%, to 0.56 cm in trees surviving attack (table 2). In one sample pair (no. 10), radial growth of the poor vigor tree was greater than that of the healthy tree, even though the sapwood was extensively stained with fungus. The poor vigor tree in pair no. 10 was considerably younger than those in other pairs (table 1), but it is not known if this age difference was a factor in the rapid growth observed for the tree. If pair no. 10 is excluded from the data, the growth reduction for the poor vigor trees was even greater—41%.

A comparison of crown vigor rating with a count of pitch tubes on the lowest 4 m of the bole is shown in figure 2. Trees with ratings of 1 or 2 generally had more

Table 1.—Age, diameter at breast height, height, and presence of pitch tubes for paired ponderosa pine trees having good or poor vigor.

Pair No.	Age Good	Age Poor	d.b.h. Good	d.b.h. Poor	Height Good	Height Poor	Resin Clusters[1] Good	Resin Clusters[1] Poor
	years		*centimeters*		*meters*		*number*	
1	75	80	16.0	19.9	9.0	9.0	0	7
2	65	61	14.6	19.6	6.0	8.0	0	9
3	59	56	14.7	20.0	8.0	10.0	0	7
4	59	56	33.1	20.6	9.5	9.5	0	40
5	56	51	13.5	20.6	8.0	10.0	0	40
6	59	60	26.4	24.8	11.0	11.0	0	70
7	55	71	27.4	40.0	11.0	12.0	0	70
8	73	77	16.5	22.3	9.5	9.5	0	39
9	37	56	13.4	18.0	8.5	10.5	0	22
10	58	38	27.9	20.0	9.0	8.5	0	14
Mean	59.6	60.6	20.3	23.1	9.0	9.8	0	31.8

[1]*Number of resin clusters observed on the bole between 1 and 2 m above the ground.*

Table 2.—Sapwood infection, foliage, and radial growth characteristics of paired ponderosa pine trees having good or poor vigor

Pair No.	Clear sapwood[1] Good	Clear sapwood[1] Poor	Branch length with live needles[2] Good	Branch length with live needles[2] Poor	Needle length[2] Good	Needle length[2] Poor	Needles[2] Good	Needles[2] Poor	Age of oldest needles Good	Age of oldest needles Poor	5-year radial growth Good	5-year radial growth Poor
	. . . . percent		*. . . . . centimeters . . . .*				*. . . . . no./cm . . . . .*		*. . . . . years . . . . .*		*. . . centimeters . . .*	
1	100	67	18.5	16.5	12.0	12.0	34.4	38.2	5.5	5.0	0.69	0.45
2	100	63	35.0	14.5	13.2	11.5	24.8	30.1	5.5	5.5	0.69	0.43
3	100	89	37.5	12.5	11.5	9.0	25.2	17.7	6.0	4.0	1.32	0.70
4	100	67	35.0	8.0	13.5	9.8	26.6	16.5	6.0	3.5	1.06	0.60
5	100	100	37.5	12.0	12.5	10.0	19.3	19.8	6.0	5.0	0.52	0.48
6	100	77	31.0	7.5	13.5	11.5	20.6	22.8	6.5	5.0	0.80	0.41
7	100	99	34.0	14.5	14.5	11.7	23.6	29.1	6.0	4.5	0.58	0.39
8	100	76	19.0	9.0	13.0	10.5	26.9	24.3	6.0	5.0	1.04	0.44
9	100	86	18.5	8.0	11.5	9.0	19.6	21.7	5.5	4.0	1.10	0.72
10	100	20	31.5	6.0	13.5	10.0	42.6	32.0	5.0	5.0	0.68	0.93
Mean	100	74.4	29.8	10.8	12.9	10.5	26.4	25.2	5.8	4.6	0.85	0.56
Significance[3]	*		*		*		N.S.		*		*	

[1]*Each value is the mean for four increment cores collected at breast height (1.4 m).*
[2]*Each value is the mean for two branches sampled on each tree.*
[3]*Asterisk indicates statistically significant difference between means of the 1% level of probability.*

than 10 pitch tubes. In contrast, trees with ratings of 4 or 5 had no pitch tubes in 9 of 10 trees.

Discussion

The findings presented here support the hypothesis that the poor vigor of ponderosa pine trees surviving a mountain pine beetle attack is a direct result of a partial disruption of the sapwood conducting system by blue-stain fungi. In most of the poor vigor trees, blue-stain fungus was observed in a portion of the sapwood. The hyphae of blue-stain fungi generally pass through simple or bordered pits (Boyce 1961). Bordered pits are the chief pathway for water flow in sapwood tracheids, and their blockage by hyphae appears to restrict water flow in the transpiration stream (Mathre 1964).

The percentage of sapwood infected by blue-stain fungi in the increment core samples varied considerably. The samples were collected at only one height on the tree, and only four cores were taken. Undoubtedly, the percentage of sapwood infected varies along the length of the bole, so that sampling at one height and with increment cores rather than cross sections yields highly variable estimates of sapwood infection. All that is necessary for a restriction in water supply to the crown is for sapwood to be partially blocked somewhere along the bole. Sapwood samples collected at other heights from poor vigor trees in pair no. 5 and pair no. 7 (table 2) might reveal more extensive fungal involvement.

It appears from data in table 2 that the functional loss of roughly 25% of the conducting sapwood is adequate to cause a drastic reduction in the amount of foliage that

can be supported physiologically. A reasonable estimate of the relative leaf area of good and poor vigor trees may be obtained by calculating the total needle length per branch. Needle diameter and the number of live branches in the crown appeared to be similar in both the attacked and unattacked trees.

As an estimate of relative needle area, total needle length per branch was calculated as the product of branch length with live needles, needle length, and the number of needles per centimeter (table 2). Good vigor trees had 10,149 cm total needle length per branch, whereas poor vigor trees had 2,858 cm total needle length, roughly 70% less than on healthy trees.

Recovery from the mountain pine beetle attack had not begun at the study site by the time of sampling. There was no evidence that either the amount of foliage produced or the radial growth of the sapwood was increasing in recent years. In fact, observations during June 1984, 1 year after data were collected, indicated both the loss of all foliage from lower branches of several severely attacked trees and the death of several other severely attacked trees. Recovery from a sudden loss of sapwood conducting tissue is very different from loss of foliage by causes such as insect defoliation. The recovery of total foliar surface occurs as rapidly as new foliage is produced, if defoliation does not continue.

In the case of sapwood blockage, however, long-term radial growth is required to replace sapwood lost by irreversible blockage. This requires many years of radial growth; and with the depleted foliage area, annual radial growth is low. Consequently, full recovery may take several decades if it occurs at all. It is unclear whether the additional decline and occasional death of severely attacked trees noted in 1984 was the result of progressive blue-stain fungal infection or if other factors reduced tree vigor.

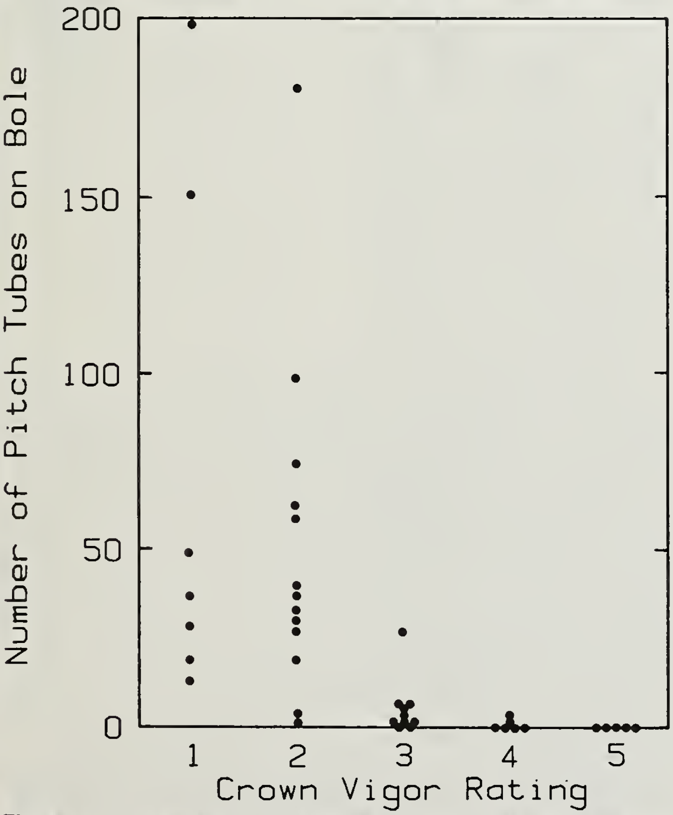

Figure 2.—Comparison of the number of pitch tubes on the lower 4 m of bole with the visual rating of crown vigor.

Salvage logging may be useful after a mountain pine beetle epidemic in ponderosa pine, both to recover the merchantable wood and to reduce the wildfire fuel load. Because of the questionable and very lengthy recovery time of surviving attacked trees, poor vigor trees should be considered for removal at the time of salvage, unless other factors (e.g., high individual tree value) are involved. Removal of poor vigor trees will facilitate the development of both the remaining healthy trees and newly established seedlings.

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